Why *Sesamia nonagrioides* (Lefèbvre) (Lepidoptera : Noctuidae) is a pest only in portions of its geographic range: the influence of climate.

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Abstract. The stem borer *Sesamia nonagrioides* (Lefèbvre) (Lepidoptera : Noctuidae) is a major pest of maize in Mediterranean Europe and in several countries of sub-Saharan West Africa but not in East Africa where it lives on wild host plants along wet places. Sampling of *Sesamia* species in maize fields in Côte d'Ivoire during five years revealed high densities of *S. nonagrioides* in the southern forest regions, and showed that it was absent in crops in the northern half of the country, a savannah region where *Sesamia calamistis* was the major pest. A regression analysis showed that rainfall and temperature explained 81% of the variation of the density of *S. nonagrioides* in maize crops. The model predicts no infestation in the cool and dry conditions of East Africa. This conclusion is in agreement with the results of the study of migration from mitochondrial genes that showed that the species moved highly only along wet places in East Africa. In southern France, where *S. nonagrioides* is a pest of maize, the model predicts no infestation. This contradiction may be explained by (i) the selection of individuals adapted to cold and dry climate, (ii) The diapause, that occurs only in the palearctic region and (iii) the possible diffusion by humans. Heavy damage in maize crops by this pest in France are mentioned only from 1836, and were not mentioned in a comprehensive book on maize by Parmentier in the late eighteenth century. The colder temperatures of the little ice age may explain that no infestation occurred in maize fields at that time. In West Africa, *S. nonagrioides* is absent in the countries East of Togo in spite of favourable climate, which is likely due to the Dahomey gap, a dry region that splits the forest.

1. Introduction

The maize stem borer *Sesamia nonagrioides* (Lefèbvre) (Lepidoptera : Noctuidae), has a wide and fragmented geographic distribution that extends over Mediterranean Europe, Northwest Africa and equatorial and tropical regions of sub-Saharan West Africa and East Africa.

The taxa on either side of the Sahara were first considered different species, *S. nonagrioides* and *Sesamia botanephaga* Tams & Bowden [1]. Later on Nye [2] observed that their morphology was nearly identical and named them two subspecies, a status that was recently still regarded as uncertain [3]. Molecular data enabled to conclude that these taxa do indeed belong to the same species but that they must not be regarded as sub-species [4]. Actually, in the sampled regions, Europe and sub-Saharan Africa, the species includes three geographically isolated populations. In sub-Saharan

Africa, the West and East populations were separated a long time ago, estimated at 1 Myr from the mitochondrial distance of 2.3%. The fragmentation between the African and European populations is much more recent and it was shown that the most plausible hypothesis is that the species crossed the Sahara during the Last Interglacial, about 100 kyr ago [4]. This was the first study that showed the considerable influence of abiotic factors on the distribution of this insect, that was able to colonize new continents when climate became warmer and wetter.

Sesamia nonagrioides is a rather generalist species unlike the most part of the other species of the subtribe Sesamiina which are specialized on one or very few host plants [5-8]. Larvae of *S. nonagrioides* feed in the stems of many Poaceae, Cyperaceae and Typhaceae [2, 9]. This nutritional plasticity suggests that host plants must not have a major influence on the distribution and abundance of this species, contrary to more specialized species which have, for the most part, a localized distribution [6-8]. In contrast, several observations suggest that the influence of abiotic factors on this widely distributed species might be strong. For instance, *S. nonagrioides* is a major pest of maize in several countries of West Africa [10-12] but not in East Africa. For example in Kenya, where maize is one of the main crops, this pest is very rarely or not at all found in fields [13-14]. These differences in abundance might be a consequence of abiotic factors. In Europe, to be able to survive, this tropical species had to adapt to climatic conditions very different from those in its region of origin. An example of this adaptation is the diapause during cold months, which does not occur in the tropics. Diapause enables a better resistance to hard winter conditions but within certain limits only. *Sesamia nonagrioides* is indeed restricted to the Mediterranean regions, at latitudes lower than 45° North in France [9]. Temperature therefore has likely a strong influence on this species in Europe. Furthermore, *S. nonagrioides* has apparently not always been a major pest of maize as it is currently. Indeed, in an exhaustive report on maize in France in the late 18th century, the famous agronomist Parmentier did not mention any borer damage [15]. The species was described only in 1827 [16], but its damage in the stems and cobs is easily visible and should have been observed in case of strong infestation. Parmentier lists several other pests (insects and fungi) known by their local name only, some of them less damaging than *S. nonagrioides*. If this species was present in Europe at that time, as is suggested by genetic data [4], the question arises as to why it would not have infested maize in southern France, and particularly whether this might be due to climatic factors.

The aim of the present paper is to gain a better insight into the influence of these factors on the distribution, abundance, and pest status of *S. nonagrioides*.

2. Materials and Methods

2.1. Population density in Côte d'Ivoire

During five years, from 1986 to 1990, the population density of *Sesamia* species has been estimated in maize fields grown in the various ecological zones of Côte d'Ivoire. In this country, rainfall decreases from the southern forest region (about 2000 mm/year) up to the northern savannah region (900-1000 mm/year) (Fig. 1) (modified from [17]). Concomitantly, there is a strong reduction in relative humidity, from 85% to 65%. Temperature decreases from East (annual average of about 26°C) up to West (24-25°C) (Fig. 1). The country is divided into two main ecological zones (Fig. 2). The Guinean zone, roughly the southern half of the country, is a region of forests, and is divided in three sectors. The southern part, the Ombrophil sector, is a region of evergreen forest; the northern part, the preforest sector, is a transition region and comprises of a forest-savannah mosaic; between both, the Mesophil sector is a region of semi-deciduous rain forest [18]. The Sudanese zone, roughly the northern half of the country, is drier; it is the savannah region, which becomes drier from its southern part, the sub-Sudanese sector, to its northern part, the Sudanese sector. Altitude is low in Côte d'Ivoire, less than 400 m, except along the western border, from Man up to the North, where it is between 500-900m, with peaks of more than 900 m surrounding Man [19].

The population density and relative proportions of *Sesamia* species were estimated in maize crops planted in June-July, the only ones that can be grown at the same time in the North of the country, where there is only one rainy season per year, and in the other regions. Several hundred plants were sampled in each location, between the soft dough stage and maturity (at about 80 days after emergence, 20 days before maturity), at the peak of borer density. The insects collected after dissection were reared until the adult stage and identified. In two southern localities, San-Pédro and Abidjan, only the proportion of the different *Sesamia* species was estimated because the maize crops could not be planted at the same dates as in the other regions.

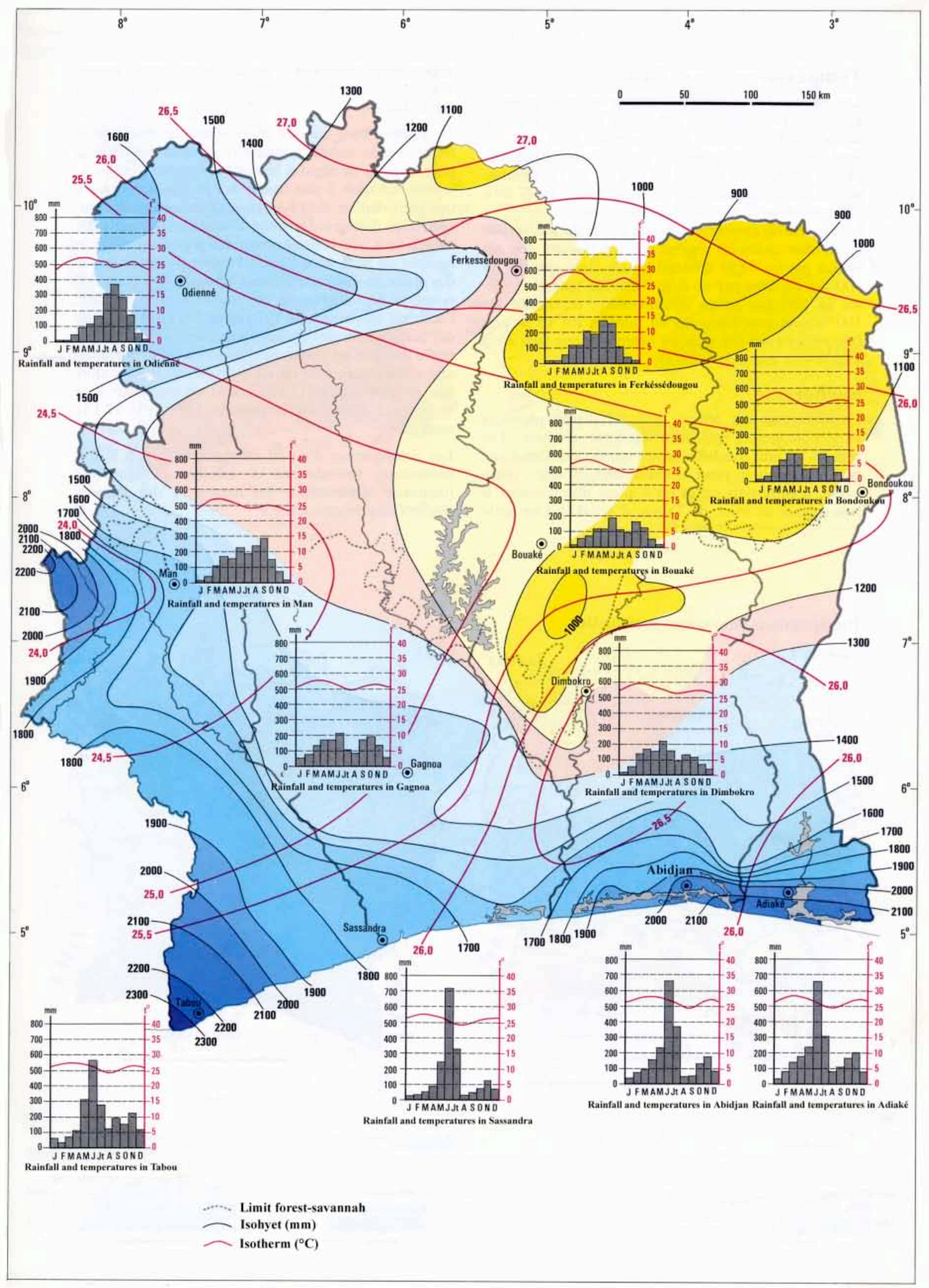

Figure 1. Annual rainfall and average temperature in Côte d’Ivoire (1961-1975) (modified from [17]).

2.2. Gene flow between populations

In order to examine whether the differences in maize infestation might result from variable migratory ability, gene flow between populations was estimated within West Africa and East Africa. In West Africa, three populations were sampled (Fig. 4), in Côte d'Ivoire (35 individuals), in Ghana (21 individuals) and in Togo (four individuals). In East Africa, five populations were sampled in Kenya: three in close localities next to Lake Victoria (31 individuals), one in the Rift Valley (three individuals) and one to the East of the Rift Valley (eight individuals) (Fig. 4).

Sequence data were obtained from a fragment of the mitochondrial gene Cytochrome b (915 nucleotides). Total DNA was extracted using a Qiagen DNeasy tissue kit (Qiagen GmbH, Germany) and the gene was amplified by Polymerase Chain Reaction (PCR) using the successive steps: initial denaturation for 5 min at 92°C; 39 cycles of denaturation for 1 min at 92°C, annealing for 1.30 min at 46°C, extension for 1.30 min at 72°C; and final extension for 5 min at 72°C. The reaction mixture contained 3 mM $MgCl_2$, 0.4 μM primers, 0.24 μM dNTPs, 2 U of Promega *Taq* polymerase and 100 ng of DNA per 50 μl of reaction mixture. The primers used were CP1 (5'-GATGATGAAATTTTGGATC-3') (modified from [20]) and TRs (5'-TCTATCTTATGTTTTCAAAAG-3') [21]. The PCR product was then purified using the Qiagen QIAquick PCR purification kit (Qiagen GmbH, Germany). Sequencing reactions were carried out using the Sanger dideoxy method [22], and, finally, sequences were run and detected on an ABI 377 automated sequencer.

The migrant number between populations per generation (Nm) was calculated following Slatkin's method [23] using Arlequin software ver 3.1 [24]: one individual exchanged between two populations indicates a gene flow sufficient to prevent the fixation of neutral alleles [25].

3. Results

3.1. Population density in Côte d'Ivoire

Three *Sesamia* species were collected in maize fields in Côte d'Ivoire (Fig. 2). *Sesamia penniseti* Tams & Bowden was very rare; only some individuals were found in Bouaké, in the centre of the country. This species feeds in fact mainly in a wild host plant, *Pennisetum purpureum* [8] and is not a major pest of maize. *Sesamia calamistis* Hampson was dominant in the savannah regions, in the preforest sector and in the western part of the Mesophil sector (Figs. 2 & 3). *Sesamia nonagrioides* was dominant in the eastern Mesophil sector and in the Ombrophil sector where its proportion got up to nearly 100% (Figs. 2 & 3).

The populations of *S. nonagrioides* decreased from the South up to the North and from the East up to the West (Fig. 3). The proportion of this species increased however again in Man, in the western region of high altitude and heavy rainfall. *Sesamia nonagrioides* was not found in the preforest sector, in Brobo and Bouaké (Figs. 2 & 3). However it was found, though at very low density, in the North of the country, in Ferkéssédougou, in a site surrounded by large areas of irrigated rice.

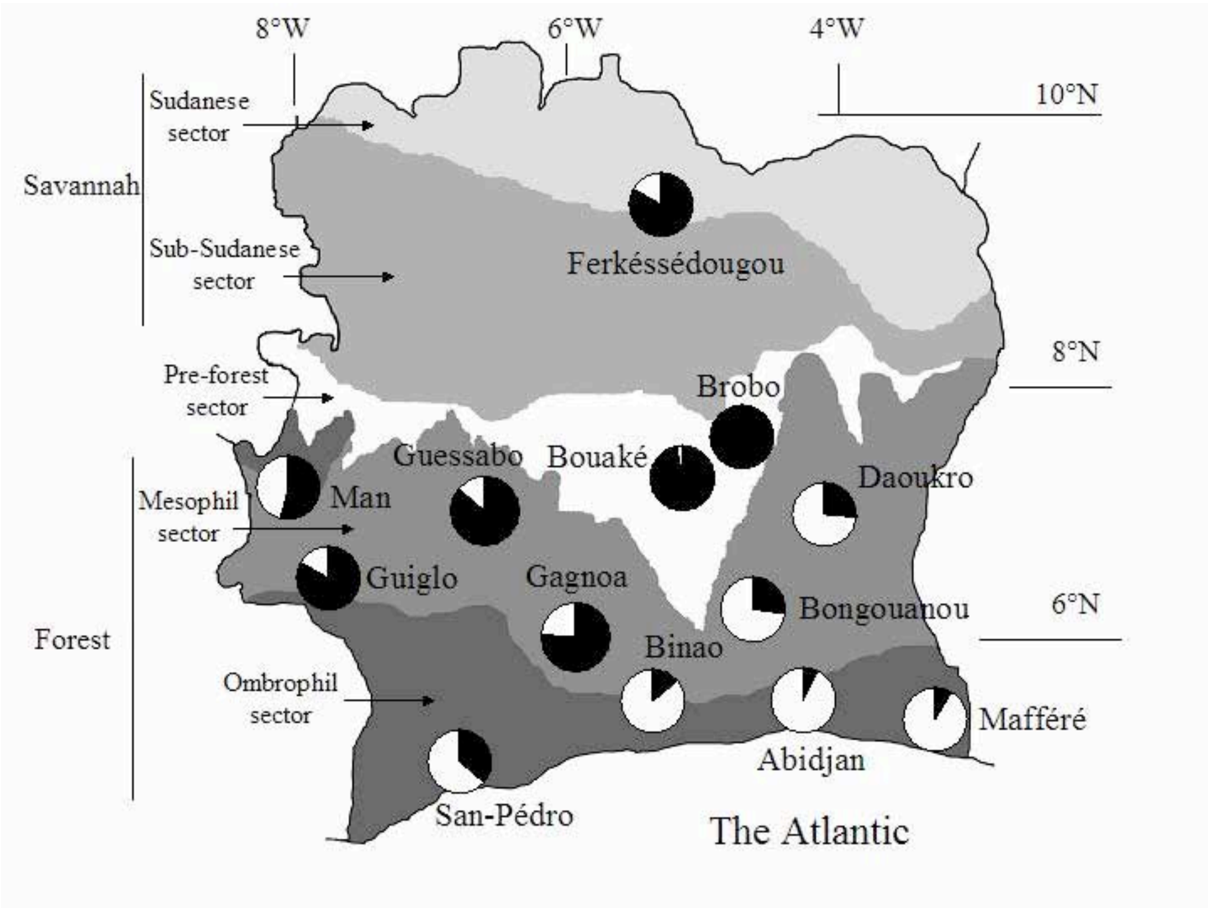

Figure 2. Proportion of the *Sesamia* species in maize fields in the different ecological zones of Côte d'Ivoire. Black: *S. calamistis*; white: in Bouaké *S. penniseti*, in the other localities *S. nonagrioides*.

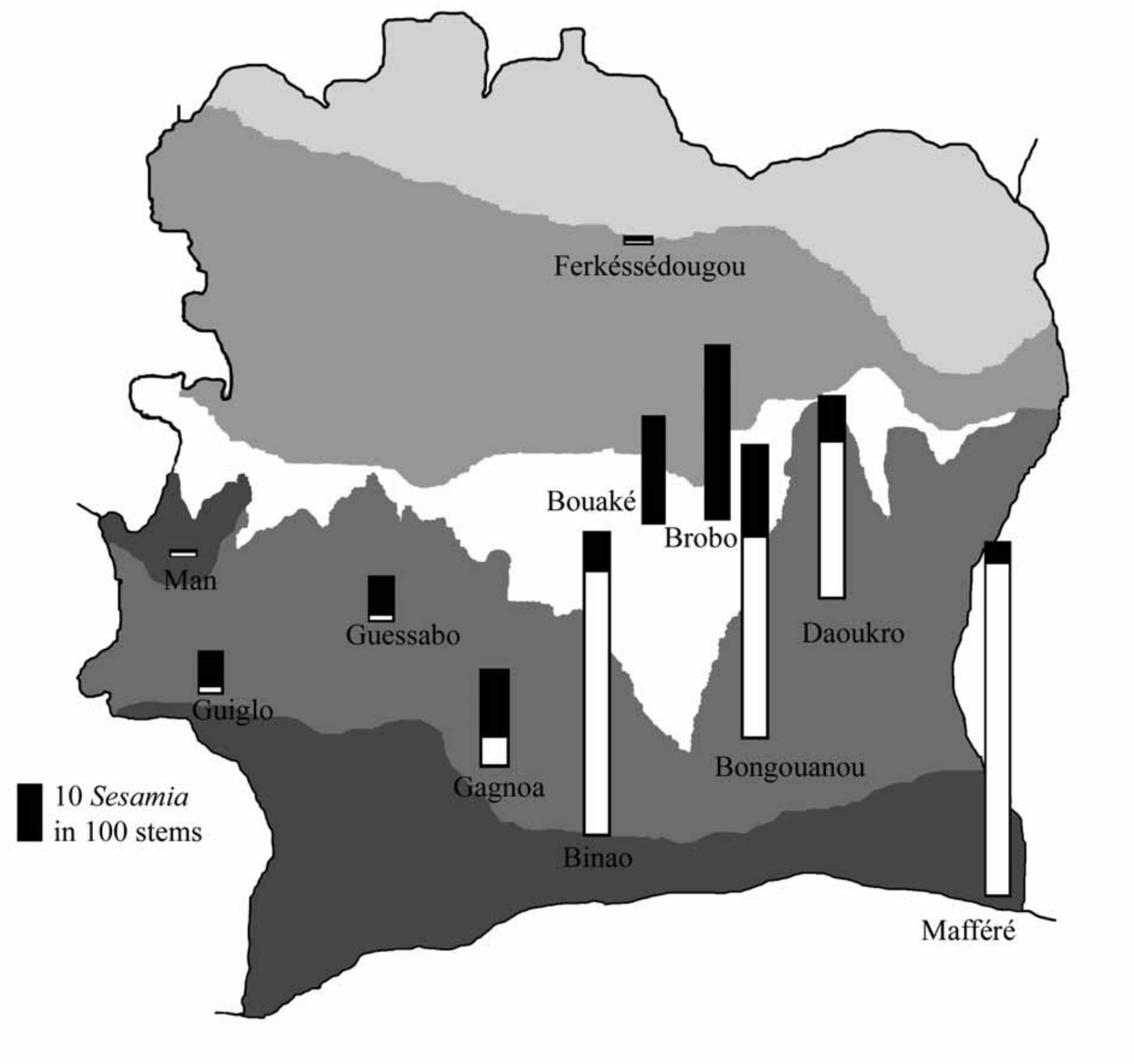

Figure 3. Density of *Sesamia nonagrioides* (white) and *S. calamistis* (black) in maize fields in Côte d'Ivoire.

The comparison of the densities of *S. nonagrioides* to climatic conditions in Côte d'Ivoire suggest both might be correlated. Indeed, rainfall and relative humidity increase southwards and temperature increases eastwards, similarly to the populations of the pest. Although these climatic averages are not those of the sampling years, the characteristics of climate in Côte d'Ivoire are rather constant, i.e. more humid in the forest regions of the South and colder in the mountain regions of the West, so these averages over 15 years (1961-1975) may safely be considered representative of climate during the sampling years, or at least of the differences between regions.

A multiple regression analysis of the population density on annual rainfall and average annual temperature was therefore carried out (Table 1). It is significant and explains 81% of the observed variation in density. Both factors have a significant influence.

Table 1- Regression analysis of the density of *S. nonagrioides* on rainfall and temperature

Explanatory variable	Coefficient	P(>|t|)
Constant	-529.23	0.0005
Annual rainfall (mm)	0.043	0.0017
Average annual temperature (°C)	19.01	0.0007
Multiple R^2	0.81	
$P(>F_{2,8})$	0.0014	

3.2. Gene flow between populations

The migrant number per generation between the different countries of West Africa is high in spite of geographic distances up to 500 km (Table 2). In contrast, in East Africa, high gene flow occurs only between the localities next to Lake Victoria distant from about 50 km at most (Table 3).

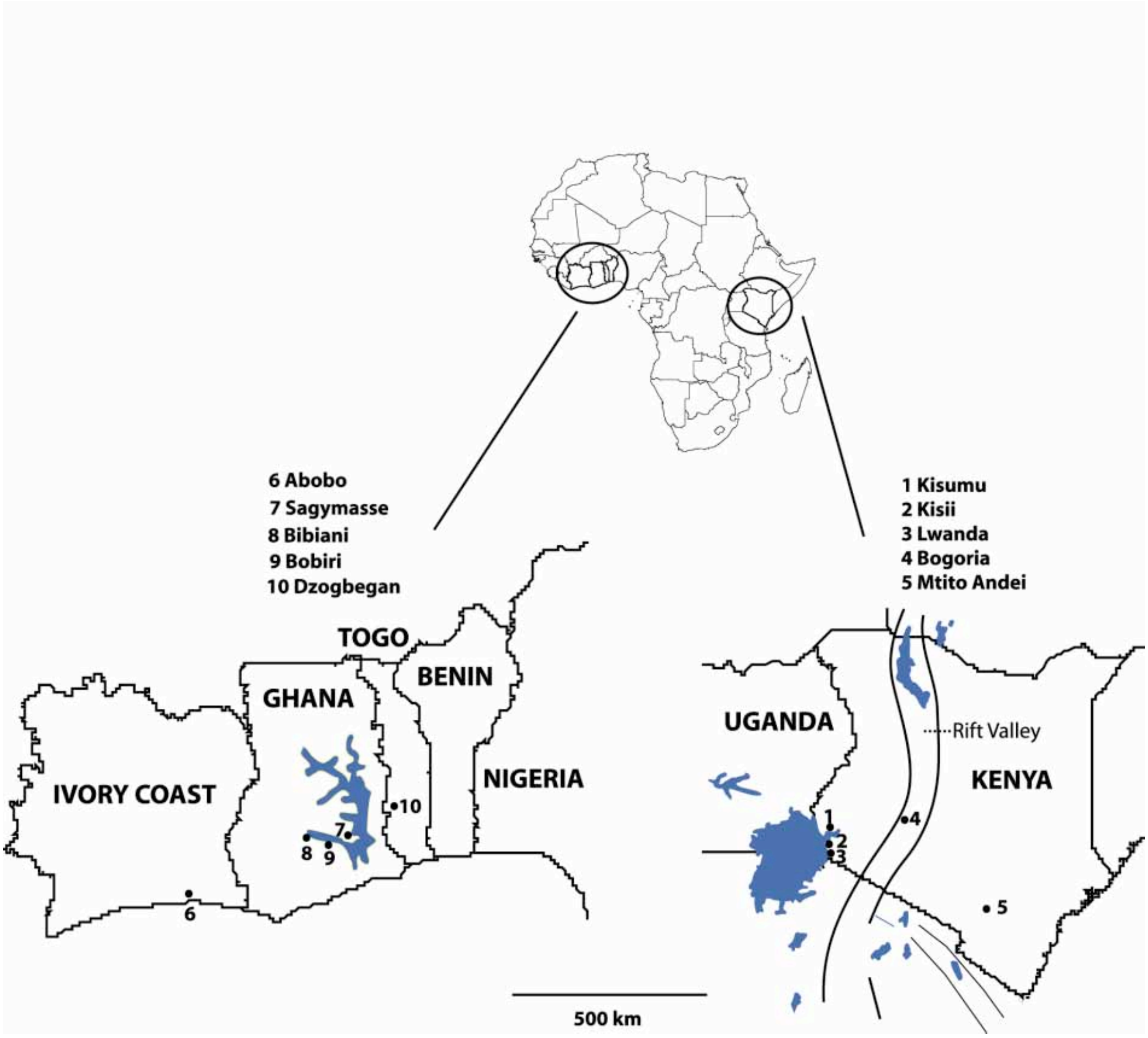

Figure 4. Gene flow study: localities sampled in West Africa and East Africa.

Table 2- Number of migrants per generation (Nm) (below diagonal) and geographic distance (km) (above diagonal) in West Africa

	Côte d'Ivoire	Ghana	Togo
Côte d'Ivoire	-	269	564
Ghana	2.42	-	250
Togo	Infinite	13.11	-

Table 3- Number of migrants per generation (Nm) (below diagonal) and geographic distance (km) (above diagonal) in East Africa (Kenya)

Locality	Kisumu	Kisii	Lwanda	Bogoria	Mtito Andei
Kisumu	-	57	51	166	472
Kisii	7.02	-	8	211	470
Lwanda	3.55	59.60	-	209	477
Bogoria	0.51	0.67	0.89	-	373
Mtito Andei	0.19	0.23	0.23	0.08	-

4. Discussion

The results showed that temperature and rainfall explained a great part of the variation in the density of *S. nonagrioides* in maize crops in Côte d'Ivoire: the greater these two abiotic factors, the higher the pest density. In this respect *S. nonagrioides* differs from the other maize borers as it is the only species whose populations increase highly in the Ombrophil sector. All the other species, i.e. the stem borers *Busseola fusca* Fuller (Lepidoptera: Noctuidae), *Sesamia calamistis*, *Eldana saccharina* Walker (Lepidoptera: Pyralidae), and the cob borer *Mussidia nigrivenella* Ragonot (Lepidoptera: Pyralidae), are adapted to less humid conditions and have population densities lower in the Ombrophil sector than in the Mesophil sector [26].

Sesamia nonagrioides is therefore a species particularly well adapted to wet and hot climate. In such climatic conditions high gene flow was observed between populations in West Africa. In contrast, in East Africa, in Kenya, the species is found only in riverine and swampy places. High gene flow was observed only between the populations surrounding Lake Victoria which were at the most 50 km apart.

In Kenya, climate is dry and cool, which may explain that migrations are limited to the surroundings of wet places, and that maize fields are not infested. Indeed, if we apply the regression equation fitted for Côte d'Ivoire to Kenyan climatic data, the estimated densities in maize fields are negative, which means not different from zero (Table 4).

Table 4. Average rainfall and temperature, and estimated density of *S. nonagrioides* in maize fields in Kenya

Locality	rainfall (mm)	temperature (°C)	Estimated density per 100 plants
Kisumu	1224	22	-58
Bogoria	862	16	-188
Mtito Andei	630	22	-84

These results enlighten therefore the major influence of abiotic factors on the pest status of *S. nonagrioides* in sub-Saharan Africa, and enable to explain the absence of this species in maize crops grown in dry and cool places while it may be found along rivers or in swampy places nearby.

It must however be emphasized that the most significant explanatory variable might not have been included in the analysis, because it was not available. Indeed, in spite of low rainfall in East Africa, *S. Nonagrioides* survives and migrates along wet places; this means that the most important variable might be relative humidity. The females of the species need likely a very high humidity during night to lay their eggs as well as to migrate. This high relative humidity is found only along wet places in East Africa whereas it is found throughout the forest regions in West Africa, where rainfall is high, particularly in the ombrophil sector.

In West Africa, however, *S. nonagrioides* is not present everywhere even if climatic conditions are favourable. In particular, it is not a pest of the maize crops grown in the forest region in southern Nigeria. For instance, Bosque-Perez & Mareck [27] did not find the species in Benin City where climatic conditions are wet and hot (Annual Precipitation = 2074mm ; Annual average temperature=26.1°C) and where maize infestation should be high (density estimated by the regression equation: 56 larvae in 100 stems).

Buadu *et al.* [12] put forward the hypothesis that the absence of *S. nonagrioides* to the east of Togo might be due to the Dahomey gap, a region that stretches from South-East Ghana to South Benin and which is too dry to enable the implantation of forest. It is very likely that, nowadays, this savannah region is a barrier to the species. However the Dahomey gap is recent. The fragmentation of the West African forest is estimated at only 3-4000 years, while from 8000 to 4000 years BP the forest extended from Liberia up to Central Africa [28-29]. From genetic data it was estimated that the fragmentation between the East African and West African populations of *S. nonagrioides* occurred about 1 Myr. Therefore, the occurrence of the Dahomey gap should have led to the division of the West African population into two sub-populations, and the species should be present in the eastern part of the forest too.

However, even if climatic conditions are favourable, the colonization of new environments by *S. nonagrioides*, particularly by females, may be rather slow. For instance, it was concluded that, in Europe, its expansion from Spain in the early Holocene, that lasted about 3000 years, was too limited to enable the crossing of the Alps, between France and Italy [4]. A similar situation might have occurred in West Africa where, during the Last Glacial Maximum, the forest survived only in a small refuge in Southeast Côte d'Ivoire [28] which was entirely isolated from two other forest refugia, in Liberia and in Central Africa. If we suppose that the populations of *S. nonagrioides* survived only in the Ivorian refuge, it is possible that their expansion during the following hot and wet period was too slow to enable colonization of Nigeria before the forest was fragmented again. Although the Dahomey gap does not seem to have had much influence on the distribution of most species, apparently the fragmentation of the forest block has occurred recurrently in this region since the end of Pliocene [28]. Therefore, if the periods without forest fragmentation were too short to enable a wide expansion of *S. nonagrioides*, it might explain that the species never reached Nigeria.

The recent history of forest fragmentation in West Africa raises however the matter of the underlying signification of the gene flow detected between the countries. Indeed, the sequence similarity might be due to recent common ancestry. If the West African population results from the expansion of the population that survived in the Ivoirian refuge during the last glaciation, then the genes may be similar not because of present gene flow but because they have had little time to evolve since this recent event. Further studies are necessary to evaluate the respective part of present gene flow and of common history in the distribution of alleles in West Africa. However, whatever the cause is, the data indicate that long migrations have occurred in West Africa, which shows that climatic conditions are suitable, whereas in East Africa, populations remain isolated and are unable to move away from wet places.

In Mediterranean Europe, climate is very different from that in sub-Saharan Africa. For instance, in Bordeaux, which is at the northwest limit of the distribution of *S. nonagrioides*, the average annual temperature and the annual rainfall are 12°C and 850 mm, respectively; the average temperature of hot months, from May to September, during which insect activity is maximum, is 18°C. In Toulouse, in the centre of the distribution area, these values are 12°C, 670 mm and 18.4°C, respectively and in Avignon, in South-East France, 14°C, 670 mm and 20°C, respectively. With such dry and cold conditions *S. nonagrioides* should not be a pest of maize according to the regression equation. The fact that it does infest maize crops suggests that it managed to adapt to these hard conditions, in particular through the selection of the most resistant individuals during winter. Two other factors may also explain this pest status in Europe. The first one is diapause. In the dry regions of Africa there is no diapause and the species cannot survive the dry season except in wet places; in Europe, diapause enables to survive the cold season in the farms where the adults find new maize plantations when they emerge in spring. The second factor is the human influence. Diffusion of the species from farm to farm may have resulted from transportation of maize stems or cobs by farmers or traders. Maybe only the fields near rivers were initially infested and transportation of maize resulted in the diffusion of the species which managed to survive locally thanks to diapause and to the proximity of maize fields at the emergence of adults.

The equation fitted from African data is therefore not valid in Europe. However, the present northern limit of the distribution may help to understand why *S. nonagrioides* was not mentioned as a pest of maize in southern France by Parmentier in 1785 [15]. *Sesamia nonagrioides* hardly survives temperatures of 0°C [30], and its mortality during hard winters is high, for instance 91% in 1981 in Avignon [31]. This is the reason why the species is absent or very rare to the north of the latitude of Bordeaux [32]. Now, temperatures at Parmentier’s time were much lower than presently. Indeed, during the period from the mid 16th century to about 1820, known as the “Little Ice Age” in Europe, temperatures were 1-2°C lower than during the following decades (e.g. [33-34]), i.e. similar to those that are recorded nowadays about 400 km northwards. Therefore, the northern limit of the distribution of *S. nonagrioides* was much more southwards than it is presently. In these conditions, the populations were probably highly reduced during hard winters, survived only in the hottest regions, were not able to increase highly during summer, and were more sedentary due to cold temperatures. Thus, damage in maize fields was probably scarce.

Later on, the increase in maize surfaces may have also contributed to turn *S. nonagrioides* into a pest. Indeed, Parmentier's book aimed at promoting maize cultivation, which was little practised at his time in France. Maize plantations began to develop highly in southern France only in the early 19th century [35]. The combined increase in temperature and in maize plantations likely led to the emergence of this new pest. *Sesamia nonagrioides* was discovered for the first time in France by Rambur in 1836 [36] in highly infested maize fields, at a time of climate warming [34].

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